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PSYCHE

VOL. XLVIII MARCH, 1941 No. 1

THE GENERAL MORPHOLOGY OF THE FEMALE REPRODUCTIVE SYSTEM OF A VIVIPAROUS ROACH, *DIPLOPTERA DYTISCOIDES* (SERVILLE)

By Harold R. Hagan

College of the City of New York

This widely distributed roach is rather robust and broad yet only three-fourths of an inch in length. It was collected by the author and an assistant, Mr. Francis Yap, some years ago in the Hawaiian Islands. This work on it was undertaken only last summer at the Biological Laboratories, Harvard University, where facilities were provided through the courtesy of Professors C. T. Brues, A. B. Dawson and Leigh Hoadley. Acknowledgement should likewise be made for the results obtained by my colleague, Professor James I. Kendall, in photographing sections not especially favorable for photomicrographs.

The method of reproduction by this roach made an examination of the genital tract eventually inevitable though only its general conformation will be given here. Fortunately, Snodgrass (1933) has rendered the task much easier by his excellent illustrations and detailed description of these parts in *Blatta orientalis*. The reproductive systems of the two species possess similar subdivisions varying only in their shapes, relative sizes and functions. To reveal these homologies, the reproductive system of *B. orientalis* has been shown in figure 1. It will at once be seen that the vestibule has been shortened in the viviparous species to be described while, on the other hand, *orientalis* possesses the rudiments

of a genital pouch above and a brood sac below the junction of the oviduct with the genital chamber. These rudiments may have no important specific function in this species for, it will be recalled, the female is oviparous and utilizes the vestibular portion of the genital chamber for oöthecal formation and placement of the eggs within the oötheca cast there. Figure 2 gives diagrammatic dorsal and lateral views of this system in *D. dytiscoides.* The brood sac is somewhat enlarged and asymmetrical in shape for eggs with young embryos are enclosed. They are placed diagonally because their slightly narrower micropylar ends, occupying less space, are directed toward the left.

Six ovarioles comprise an ovary which is cone-shaped with the base resting on the distal end of a paired oviduct. Each ovariole tapers anteriorly to the germarium and terminal filament in the usual fashion. The former contains twenty or thirty oögonia within its lumen and there are always seven or eight clearly discernible oöcytes within the vitellarium or lower portion of the ovariole; two more than shown in the upper ovariole in the figure, for only part of the

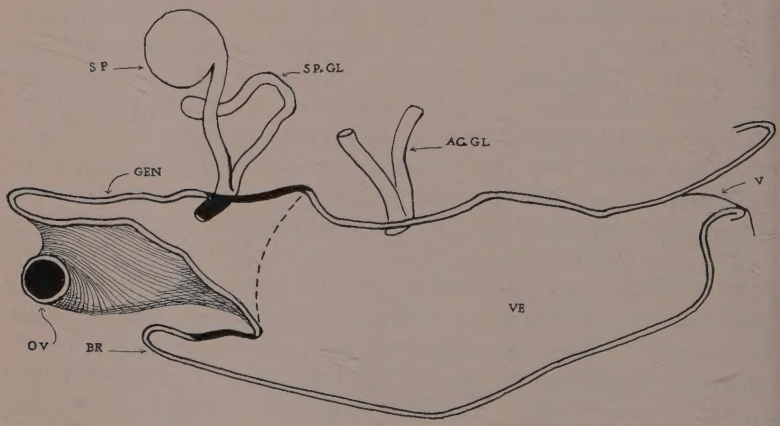


Figure 1. *Blatta orientalis.* Diagrammatic median section through the genital chamber of the female reproductive system. AC.GL, accessory gland; BR, rudiment of a brood sac; GEN., rudiment of a genital pouch; OV, cross-section of proximal end of left oviduct; SP, spermatheca; SP.GL, spermathecal gland; V, vulva; VE, vestibule. (Redrawn and relabelled from Snodgrass, 1933: Smithsonian Miscellaneous Collections, v. 89, no. 8)

seventh is visible at the left. Their panoistic arrangement and structure are typical of roaches.

The paired oviducts are short, stout tubes which convey the oöcytes from the ovaries. Each bears a slightly dilated distal end which might be termed the calyx of the oviduct. From the latter arise six terminal or subterminal urn-shaped pedicels. The lumen of the pedicel is continuous with that

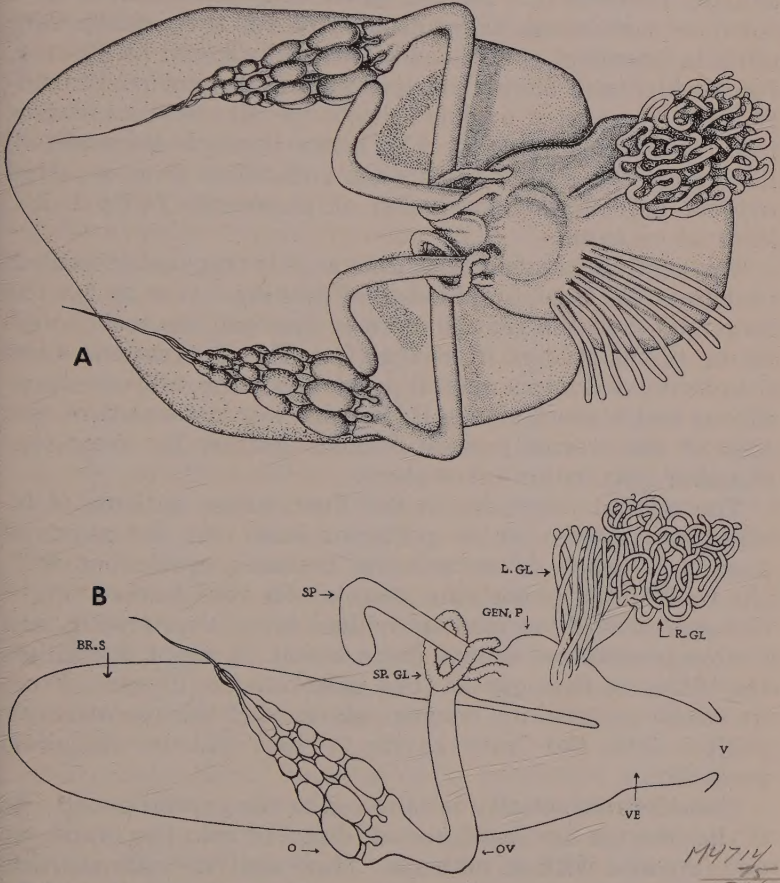


Figure 2. *Diploptera dytiscoides.* Diagrammatic views of the female reproductive system. A, dorsal aspect above; B, lateral aspect below. BR.S, brood sac; GEN.P, genital pouch; L.GL, left accessory gland; O, ovary; OV, oviduct; R.GL, right accessory gland; SP, spermatheca; SP.GL, spermathecal gland; V, vulva; VE, vestibule.

of the calyx but distally it ends blindly. The proximal end of an ovariole joins the blind end of each pedicel.

The wall of the paired oviduct is muscular while its lumen is lined by an epithelium which may be thrown into deep folds when it contains no oöcyte. Each oviduct extends a short distance ventrally and posteriorly, then bends abruptly toward the midline of the body. As the two meet each turns sharply posteriorly. At this point they are enclosed in a common peritoneum and musculature but their lumens are quite independent. This condition is illustrated by Plate 1, fig. 4 which also shows the epithelial folds previously mentioned. The united oviducts discharge almost immediately into the median oviduct. The latter is much abbreviated, lies within the wall of the atrium and differs from a paired oviduct only in the possession of a smooth, fairly thick, internal cuticula.

The genital chamber, or vagina as it is frequently termed, continues the tract to its external opening. It is by far the largest part of the reproductive system and the most interesting to the student of viviparity. The illustrations show it to be divided into a genital pouch or atrium, a brood sac or uterus and a vestibule. All bear a heavy musculature, but that of the uterine portion is much greater for from this chamber parturition takes place.

The genital pouch has a flat floor whose cuticula is irregularly folded over its posterior half. At the proximal margin it bends downward and becomes continuous with the roof of the underlying uterus. Its roof bears a slight elevation where the median oviduct joins it anteriorly, and a more pronounced central dome which, no doubt, facilitates the tilting of the eggs as they pass into the uterus. From its dorsal surface, too, various glands and the spermathecæ project into the body cavity. They will be discussed presently.

Considerable activity is centered in the genital pouch. In it the oöcytes are inseminated, directed into the brood sac and provided with an oötheca. These activities are coordinated by the operation of the valves of the ovipositor which lie in its lumen. In addition, the spermatophores from the male are deposited here till further disposition is made of their essential elements.

The uterine portion is huge compared with the rest of the tract and is capable of enormous distention during gestation. Plate 1, fig. 2 is particularly striking since fourteen developing eggs may be seen in it, while twelve is the usual number. The arrows point to two embyros which will not survive for they are forming in immature oöcytes. An empty uterus is always much folded and its cuticula and epithelium are thrown into massive fungiform papillæ. The vestibule is short, connecting with both atrium and uterus anteriorly and opening to the outside of the body by means of the posteriorly situated vulva. It is quite muscular and the intima is beset with low conical papillæ, each bearing a delicate seta.

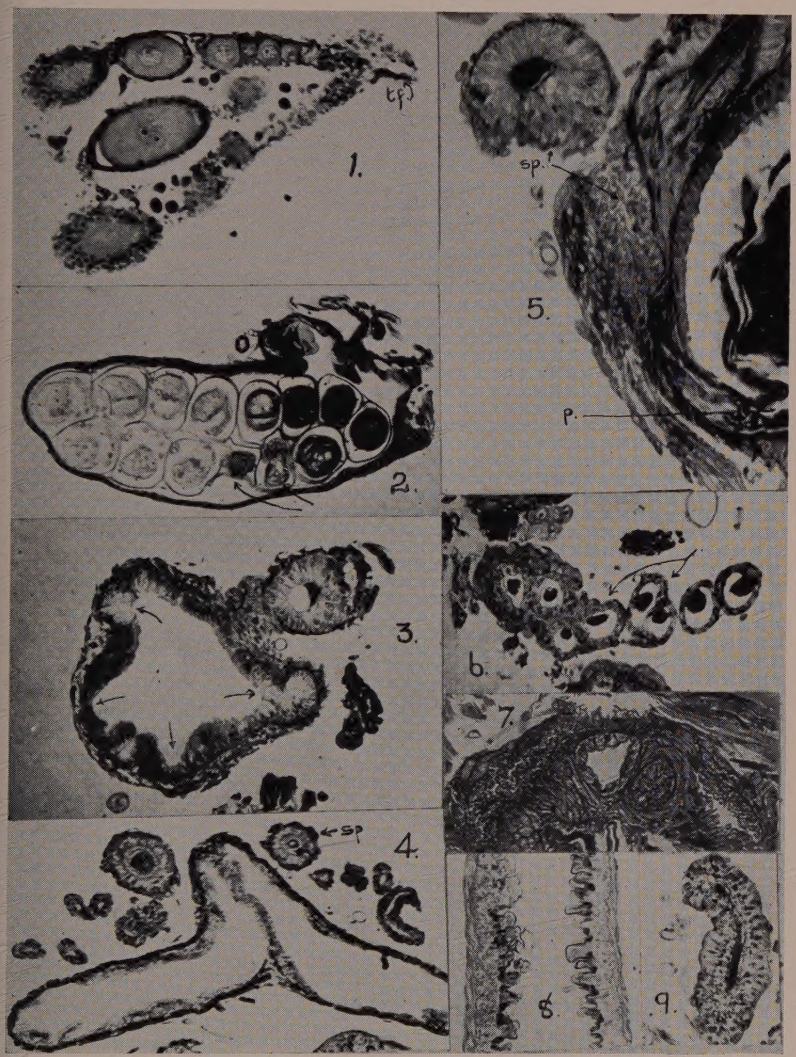
The spermathecæ are two simple, tubular glands. Each projects into the body cavity from the roof of the genital pouch on either side of the elevation formed by the insertion of the oviduct. Their muscular walls enclose a remarkably tall, columnar epithelium with a cuticula bordering the relatively narrow lumen. The spermatozoa are bent in an arc at right angles to the length of the organ, hence the oldest gametes must be situated farthest from the opening in the atrium. The proximal ends of the spermathecæ traverse the distal wall of the latter and open from papillæ above the gonopore. A laterally placed spermathecal gland entwines each spermatheca and accompanies it through the atrial wall. This gland possesses an irregular superficial outline, thick walls and a narrow lumen. The latter is constantly filled with an intensely basophilic secretion.

Posterior to the median dome in the roof of the genital pouch lie two large glands. The left one is termed a crystalloid gland for its lumen always seems to contain granular secretions. Perhaps it, too, contains the proteinaceous basal substances which form the oötheca and thus conforms to the glands studied by Bordas (1909), Ito (1924), Pyror (1940) and others. Because of its persistent secretory activity, however, it may be a nutrient organ for the embryos. Its duct, upon leaving the lumen of the atrium, widens into an ampulla or reservoir, narrows quickly again, then branches four times toward the left to produce five tubes which reach the surface of the atrium. Just at the surface each one divides again to thrust a total of ten simple tubes

straight upward into the hæmocœlar space. The arrows indicate two steps in such a division of the ducts though only eight of the ten branches are visible in Plate 1, fig. 6. Adjacent to this gland another is found to the right of the median line. Its general course is the same in the atrium but its walls are thick and the lumen practically closed. It appears in the hæmocœle as a stout column with an open lumen terminating in a calyx. From the latter arise approximately twenty very long, narrow, simple glandular tubes which coil around one another to form a compact knot. Its function is problematical. The six valvulæ of the ovipositor are approximately uniform in length yet no longer than the largest in *B. germanica*. They are, however, narrower and more delicate organs in *D. dytiscoides* than in the latter species. Two pairs are wide basally but taper distally to smoothly rounded tips. The valvulæ of the third pair are very slender throughout their length. They are not illustrated.

This, very briefly, is an outline of the female reproductive system of *Diploptera dytiscoides*. While its component elements introduce no new structures which *B. orientalis* lacks, still some of them vary greatly from the latter species that maternal care and incubation may insure viviparity. Such changes include a reduction in the number of ovarioles with a consequent limitation of the offspring to be accommodated at any one time. The lowered reproductive rate may also be associated closely with the apparent necessity for maternal nutrition of the embryos till hatching and birth, and the possible modification of the nature of the secretion from the right gland to furnish the required amount of nutriment. The oötheca, in turn, is reduced to a thin membrane which only partially envelops the egg mass and never turns brown upon contact with the products of the right gland as Pyror states is the case in oviparous species. Finally, the uterine portion of the genital chamber is definitely established as an enormous incubatory receptacle for the embryos till hatching. The maintenance of oviparous parts and accessories in the viviparous production of offspring once more recalls the old adage that "morphology is more conservative than physiology."

PSYCHE, 1941 VOL. 48, PLATE I.



Hagan — *Diploptera dytiscoides*

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Explanation of Plate 1

Diploptera dytiscoides. 1. Median section of ovary showing six follicles in an ovariole, part of a seventh, the germarium and two terminal filaments (tf). Portions of two other ovarioles are less complete. 2. The genital chamber, with genital pouch, brood sac (including 14 ova), portions of accessory glands, and vestibule. 3. Calyx of oviduct with part of one pedicel and basal attachments of others. 4. Sagittal section of paired oviducts and their junction to meet the common oviduct. 5. Cross-section of spermatheca (sp) and parasagittal section of its proximal end which terminates in a papilla (p) within the genital pouch. 6. Left accessory gland in cross-section near external surface of pouch. 7. Cross-section of left and right accessory glands as they penetrate wall of the genital pouch. 8. Fungiform papillæ lining empty brood sac. 9. Median section of portion of spermathecal gland. All figures greatly enlarged photomicrographs by Dr. J. I. Kendall.

WEST INDIAN CARABIDÆ VI.
THE JAMAICAN SPECIES, AND THEIR WINGS

By P. J. Darlington Jr.
Museum of Comparative Zoölogy

This paper is the sixth of my series on the carabid beetles of the West Indies. It is the first comprehensive treatment of the Carabidæ of Jamaica. All known Jamaican species (80) are listed taxonomically, and the list is annotated with data on the insects' wings and flight. At the end of the list, the distribution of flying and flightless species in Jamaica is summarized and discussed. The facts here put on record concerning the atrophy of wings of certain species in the mountains of Jamaica will be referred to again in a paper which I have in manuscript, on the wings of Carabidæ of mountains and islands.

The Museum of Comparative Zoölogy possesses a good representation of Jamaican Carabidæ collected by Mr. A. E. Wight, Prof. C. T. Brues, Mr. Chester Roys, and myself, and by some other persons. Besides this, I have had for study as a loan from the United States National Museum about 320 specimens of Carabidæ collected in Jamaica by Dr. E. A. Chapin and Dr. R. E. Blackwelder during the winter of 1937. This borrowed collection really provided the stimulus which has called forth the present paper. It adds several genera and species to the Jamaican list, and contains also numerous specimens taken "flying at dusk" in nets attached to automobiles. Records of species taken actually in flight are unusual, and are very interesting in connection with my studies of Carabid wings.

Species included in the following list without exact locality data are known in Jamaica only from the lowlands, below 1,000 ft. altitude, or are known merely from "Jamaica," presumably from low altitudes. Species noted as "winged" have the inner wings fully developed and apparently fitted for flight in one or more *Jamaican* specimens.

List of the Carabidæ of Jamaica

1. *Calosoma alternans alternans* (Fab.). Winged.
2. *Pachyteles sp.* Blue Mt. Peak, Dec. 13, 1890 (unique in M. C. Z.; collector unknown). This specimen has been submitted to Mr. M. Bänninger, who is not yet ready to describe it. Flightless; wings vestigial.
3. *Distichus granulipygus* Bts. Winged.
4. *Clivina dentipes* Dej. Winged.
5. *Clivina insularis* (J.-D.). Winged.
6. *Clivina biguttata* Putz. Winged.
7. *Oxydrepanus rufus* (Putz.). Winged; "flying at dusk" (Chapin & Blackwelder).
8. *Schizogenius arimao* Darl. Winged.
9. *Bembidion jamaicense* Darl. Slopes of Blue Mts. up to about 4,500 ft., along streams. Winged.
10. *Bembidion darlingtoni* Mutch. Winged.
11. *Bembidion sparsum* (Bts.). Winged; flies actively.
12. *Bembidion chevrolati* (G. & H.). Winged.
13. *Bembidion fastidiosum* (Laf.). Winged.
14. *Pericompsus blandulus* Schm. Winged.
15. *Tachys occultator* Csy. (provisional det.). Winged.
16. *Tachys bradycellinus* Hayw. Winged.
17. *Tachys carib* Darl. In Jamaica, from near sea level to about 4,500 ft. altitude, by streams. Winged; "flying at dusk" (C. & B.).
18. *Tachys abruptus* Darl. In Jamaica, from sea level to about 4,500 ft. altitude, usually by streams. Winged.
19. *Tachys trechulus* Darl. Known only from the types from Blue Mt. Forest Reserve, 5,000-7,000 ft., under deeply buried stones in damp cloudforest, *not* by streams. Flightless, wings vestigial.
20. *Tachys filax* Darl. Winged; "flying at dusk" (C. & B.).
21. *Tachys pumilus* (Dej.). Winged.
22. *Tachys striax* Darl. Winged; "flying at dusk" (C. & B.).
23. *Tachys cubax* Darl. Winged; "flying at dusk" (C. & B.).
24. *Tachys vorax* Lec. Winged.
25. *Tachys proximus* (Say). A single ♂ in the Chapin and Blackwelder collection is the first specimen of this North American species to be found in the West Indies. Winged.

26. *Tachys scitulus* Lec. Winged.
27. *Tachys* (near) *corruscus* Lec. Winged; "flying at dusk" (C. & B.).
28. *Limnastis capito* Bts. Winged; "flying at dusk" (C. & B.).
29. *Micratopus insularis* Darl. Winged.
30. *Perileptus jeanneli* Darl. Near sea level to 4,500 ft., by swift streams. Winged; "flying at dusk" (C. & B.).
31. *Perileptus minutus* Darl. Winged.
32. *Panagæus quadrisignatus* Chev. Winged.
33. *Morion georgiæ* (Beauv.). Winged.
34. *Morion costigerus* Darl. Known only from Cinchona in the Blue Mts., at about 5,000 ft. altitude, in rotten wood and under loose bark of dead trees. Flightless, wings vestigial.
35. *Agonum extensicolle cubanum* Darl. Winged.

— *Colpodes.* This is the principal genus of mountain-inhabiting Carabidæ in the West Indies: 50 species have been found in the Greater Antilles, almost all at considerable altitudes. A few of the species are winged, but the majority are flightless, with atrophied wings. Wing atrophy has evidently occurred independently in several different Antillean stocks of the genus.

36. *Colpodes cinchonæ* Darl. Known only from localities in the Blue Mts., at and above 5,000 ft., under various cover in damp forest. Wings vestigial.
37. *Colpodes faber* Darl. Known only from Blue Mt. Forest Reserve, 5,000-6,000 ft., under cover in wet forest, but (like most other Colpodes) *not* by open water. Wings vestigial, elytra ankylosed.
38. *Colpodes vagepunctatus* Darl. Known definitely only from Newton, 3,000 ft. Flightless, wings reduced.
39. *Colpodes macer* Darl. Known from Mandeville (probably mountains near), and from Cinchona in the Blue Mts., 5,000 ft. altitude. Wings vestigial.
40. *Colpodes subovalis* Darl. Known only from Blue Mt. Forest Reserve, about 5,000 ft., in rotten logs and piles of dead vegetation in damp forest. Flightless, wings reduced.

41. *Colpodes bromeliarum* Darl. From near Bath and Portland, at 300 and 1,000 ft. altitude, in epiphytic bromeliads. Winged.
42. *Colpodes roysi* Darl. Near Bath, in an epiphytic bromeliad. Winged.
43. *Colpodes punctus* Darl. Known only from Cinchona in the Blue Mts., at 5,000 ft.; habits unknown, but relationship to two preceding species suggests life in epiphytes.[1] Winged.
44. *Colpodes bruesi* Darl. Known only from Newton, 3,000 ft.; also a member of the *bromeliarum* group. Winged.
45. *Colpodes sp.* (Van Emden MS). Known only from Hartham; apparently another bromeliad species, the most highly specialized in structure of the group. Apparently winged (I have seen a specimen of this species, but did not examine the wings).
46. *Colpodes æquinoctialis* (Chd.). In Jamaica, on slopes of the Blue Mts. below 4,500 ft., along large streams. Winged.
47. *Colpodes latelytra* Darl. Known from a unique from Portland Gap, Blue Mt. Forest Reserve, 5,000 ft., from a pile of recently cut grass; the species may be arboreal. Winged.
48. *Lachnophorus leucopterus* Chev. Lowlands and slopes of Blue Mts. below 4,500 ft., by streams. Winged, flies actively.
49. *Anchonoderus subtilis* Bts. Winged, flies actively.
50. *Euphorticus pubescens* (Dej.). Winged.
51. *Perigona nigriceps* (Dej.). Winged, "flying at dusk" (C. & B.).
52. *Chlænius jamaicæ* Darl. Winged.
53. *Stenous duodecimstriatus* (Chev.). Winged.
54. *Stenous tibialis* (Chev.). Winged.
55. *Selenophorus flavilabris flavilabris* Dej. Winged.
56. *Selenophorus chalybeus* Dej. Winged.
57. *Selenophorus alternans* Dej. Winged.

[1]Since this was written, I have seen specimens of *punctus* in the Philadelphia Academy, collected by Mr. J. A. G. Rehn, definitely "from epiphytic bromeliads", "in mountain forest" at 4,980 and 5,600 ft. in the Blue Mts.

58. *Selenophorus sinuatus* (Gyll.). Winged.
59. *Selenophorus discopunctatus* Dej. Winged.
60. *Selenophorus puncticollis* Putz. Winged.
61. *Selenophorus aeneocupreus* Dej. Winged.
62. *Selenophorus nonseriatus* Darl. Winged.
63. *Bradycellus cubanus* Darl. Winged.
64. *Bradycellus velatus* Darl. Winged.
65. *Acupalpus* (*Stenolophus*) *ochropezus* (Say). Winged, "flying at dusk" (C. & B.).
66. *Masoreus brevicillus* Chev. Winged.
67. *Lebia bitaeniata* Chev. Winged.
68. *Lebia cyanea* Dej. Winged.
69. *Lebia abdominalis* Chd. Winged.
70. *Microlestes poeyi* (J.-D.). The single Jamaican specimen I have seen is winged, but *poeyi* has dimorphic wings in Cuba.
71. *Apenes marginalis* (Dej.). Winged.
72. *Apenes coriacea* (Chev.). Winged.
73. *Apenes parallela* (Dej.). Winged.
74. *Apenes aptera* Darl. Known only from Blue Mts., 5,000-7,000 ft., under stones in damp forest. Wings vestigial.
75. *Pentagonica flavipes picipes* Darl. Winged.
76. *Colliuris tetrastigma* Chd. Winged; related species fly actively.
77. *Colliuris limbatus* (Waterh.). This is the only species of Carabidæ recorded from Jamaica which is unknown to me. It is probably related to *C. picta* (Chd.), and is probably winged.
78. *Pseudaptinus apicalis* Darl. Winged.
79. *Pseudaptinus insularis* Mutch. Winged.
80. *Pseudaptinus dorsalis* (Brullé). Winged.

Of the 80 species of Carabidæ listed from Jamaica, some 63 occur in the lowlands, below 1,000 ft. altitude. All of these 63 species, in all the diverse lowland habitats, are winged. Some of them are known to fly well, and it is likely that all, or almost all, fly occasionally.

The middle slopes of the Jamaican mountains, above 1,000 and below 5,000 ft., have not yet been very thoroughly collected for beetles, but a certain number of Carabidæ have been found there. Most are winged. Half a dozen or so winged riparian species follow the mountain brooks up to an alti-

tude of about 4,500 ft., which is about as high as there are brooks in the Jamaican mountains. Some of the same species occur also along lowland streams; others are confined to the banks of the mountain torrents. Two or more winged Colpodes of the *bromeliarum* group occur on the mountain slopes, and probably live between the leaf bases of broad-leaved, pineapple-like bromeliads, in trees. And other winged Carabidæ, some of them lowland species but others perhaps peculiar, are to be expected in proper habitats on the lower and middle mountain slopes.

With increasing altitude, a few flightless Carabidæ, with reduced or vestigial wings, begin to appear among the winged ones, and from the 5,000 ft. level to the highest summit (7,388 ft.) flightless species predominate. Ten species of Carabidæ have been found at or above 5,000 ft. in the Jamaican mountains. Only 2 of the these species, both perhaps arboreal, have fully developed wings. The other 8 species have reduced or vestigial wings, and are flightless. They live chiefly or entirely on the ground in damp cloudforest.

Of course, there is still much to be learned about the details of distribution of Carabidæ in Jamaica, but the main pattern is already very clear. In the lowlands, there is a rather numerous and diverse fauna of Carabidæ, all winged. On the middle slopes of the mountains, there is a smaller, mixed, transition fauna. And at highest altitudes there is a small fauna which is predominantly flightless.

Similar conditions are found throughout the Greater Antilles (*cf.* Darlington, *Memorias de la Sociedad Cubana de Historia Natural* 13, 1939, pp. 79-80). Throughout the lowlands of each island are found numerous and diverse Carabidæ, all or nearly all of which are winged. But wherever mountains rise above 5,000 ft. a few endemic, alticoline, flightless species occur, most of them apparently derived *in situ*, independently on the different mountain tops, from winged ancestors.

This is not an accidental phenomenon. It appears to be the result of the action of powerful environmental forces. But it is difficult to say just what the forces are, for they are complex as well as powerful. I shall try to deal with them in another paper.

EXPERIMENTS IN HOUSING VESPINE COLONIES, WITH NOTES ON THE HOMING AND TOLERATION INSTINCTS OF CERTAIN SPECIES

By Albro Tilton Gaul

Brooklyn, N. Y.

During the summer of 1939 I made the following observations on some species of the Vespinæ at Lakeville, Conn. The work was not begun until early July when the wasp season had fairly advanced.

Wasp nests were captured intact, anæsthetized and transported to the laboratory for observation (1).

Hives were built to accommodate the various nests. These were wooden cases built into the open window apertures, and securely fastened and weatherstripped to keep the wasps out of the laboratory. Each hive was divided into several compartments by heavy cardboard partitions; each compartment provided a home for a single nest of hornets. The window face of the hive consisted of wire screening to admit air and light, and an adjustable aperture on the floor of the hive to control the egress of the hornets. In the laboratory each compartment was accessible through a sliding panel, with a glass observation window and a trapdoor.

Nests were placed in compartments in positions as nearly normal as possible.

When the anæsthetized colony was first placed in the hive, the aperture had to be closed to prevent the escape of the wasps. Unless this precaution were taken, the whole adult population of the nest would desert as soon as they were able to move. In one such case, the population was discovered rebuilding a nest within a few feet of the old nest site, although this was well over a mile from the laboratory. This desire to desert the nest only lasted a few hours; a colony collected in the early evening could be permitted to gather food and paper pulp next morning.

About eight hours of confinement sufficed to persuade the adults to remain with the nest and continue their normal activities.

Once established in the new environment, a colony would not voluntarily desert despite further treatment with anæsthetic. One colony of *Dolichovespula arenaria* Fab. was periodically treated with ether that I might remove a portion of the nest wall for observation purposes. These did not leave the nest although they were free to do so.

As a result of enlarging the nest, one colony of *Dolichovespula maculata* Linn. expanded the brood comb until it came into contact with the observation window in the hive. The paper nest wall was removed by the wasps and the glass served as the wall. A similar observation was figured by A. H. Clark (2). This is evidently a normal method of building the nest into contact with any surface, as nests collected from rafters and walls of buildings exhibit the same structure.

Customarily new comb is built below the existing tiers of comb. In the circumscribed space of the compartments this could not be done, so the hornets increased the area of each comb by adding cells to the periphery.

Because of the limited vertical expansion in the compartments, some of the *Dolichovespula* colonies were forced to use the floor of the hive as the nest floor, without any paper. Lacking any excavating instinct, the wasps made no effort to remove the floor of the hive.

The nests gradually assumed a hemispherical shape. In these nests, the entrance was eventually made opposite the escape aperture of the hive and on the floor of the hive.

Old wasp comb and paper was supplied to assist certain colonies in gathering paper material. None would accept this paper.

Species of *Vespula* will also respond to hive conditions without the accustomed dampness of the earth. Few notes were made on this genus as observations were made too late in the season.

Wasps returning from the fields invariably return directly to the home window. In many cases, however, they would fail to select the proper hive compartment. Even when there were two or more species in a hive, they would re-

peatedly enter the wrong compartment. This was so common throughout the season that a number of the wasps must have made the same error many times. I can only offer the explanation that the nests are never in such close proximity in nature, and that a return to within a few inches would normally bring a wasp to her nest. But in the hive, all compartments look alike, a nest odor (if any) is confused with the odor from adjacent nests, and a few inches error would send a wasp into the wrong compartment. Eventually, of course, the wasps would seek out their home nest.

The continued intrusion of wasps into the wrong compartments afforded excellent opportunities to observe the natural tolerance and animosity of the various species toward the intruders. The results are very similar to tolerance observations on Polistes (3).

In one hive were two *maculata* nests and a weakened *arenaria* nest. In this hive a returning *maculata* worker would be set upon if she ventured into the *arenaria* compartment; similarly an *arenaria* intruder would be pursued in the *maculata* compartments. Members of one *maculata* colony were permitted to enter the compartment and to walk upon the nest of the other colony; they did not enter the nest of the other colony. As a result of removing workers from the *arenaria* colony, the remaining population could no longer protect itself and the intruding *maculata* workers soon learned to steal the *arenaria* larvae as food for their own brood.

Two adjacent *arenaria* colonies in another hive permitted the same freedom of trespass on their nests as was described above for the two *maculata* colonies.

In flight outside the hives all the species were on good terms. They caused no trouble by virtue of their proximity.

To discover the outcome of a prolonged intrusion of one species in the compartment of another, I closed the escape aperture of an *arenaria* hive and placed a large *maculata* worker within the *arenaria* nest. Immediately the *arenaria* workers formed a circle about the intruder, always facing her and reminding me of the entourage of worker bees about their queen. As soon as the *maculata* moved toward the

screening in an attempt to escape, an *arenaria* worker jumped upon her back and attempted to bite off the wings, all the while flexing her abdomen in an attempt to sting the intruder. After this, several "defenders" would dart forward and nip at the legs, antennae and wings and return to the circle. This darting and biting continued until the first worker succeeded in injecting her sting, which concluded hostilities. Even after death, the intruder was worried and chewed by occasional wasps. The workers removed the dead *maculata* from the hive five days after the battle.

The *maculata* made no effort to defend itself. Aside from moving to escape, it submitted to its fate. Subsequent similar experiments with intruding *arenaria* workers on *maculata* nests resulted in the same results for the intruder.

It thus seems that members of one species of *Dolichovespula* will tolerate guests of the same species, while they are actively hostile to the intruders of another species. They are not loath to prey upon the larvae of another species and will enter the other nest to do so if permitted.

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A NEW SPECIES OF CEROPLATUS (DIPTERA, MYCETOPHILIDÆ)[1]

By F. R. Shaw

Amherst, Massachusetts

In September 1940, Dr. C. P. Alexander collected a specimen of an undescribed species of Ceroplatus on the steps of Fernald Hall at Massachusetts State College. In view of the fact that the insect was taken at Fernald Hall it was felt that species should be dedicated to the Fernalds, father and son, who founded and developed the Department of Entomology at Massachusetts State College. I take pleasure in naming this insect, *Ceroplatus fernaldi*, in honor of Professors Charles Henry and Henry Torsey Fernald.

Ceroplatus fernaldi n. sp.

Length 8 mm. General color dark brown.

Head. Vertex and occiput brown. Frons and palpi yellow. Antennae brown.

Thorax. Notum and pleurae of prothorax dark brown. Mesonotum dark brown with 3 black stripes which unite in front of the scutellum. Humeri yellow. Scutellum and pleurae brown. Hypopleurae with setae.

Wing. 5½ mm. in length. Sc_1 long ending about the distance from the humeral crossvein to the base of R_s beyond the origin of R_s. Sc_2 opposite the humeral crossvein. A dark brown spot covers R_1 and extends along R_3. Fused portion of media and radius about one third longer than the petiole of media. Veins $M_1 + _2$, M_3, Cu_1 and 2A all fail to reach the margin of the wing. Haltere yellow with a brown knob.

Legs. Prothoracic coxa brown at base, distal two thirds yellow. Trochanter yellow. Femur with a narrow brown

[1]Contribution from the Department of Entomology, Massachusetts State College, Amherst, Massachusetts.

band at base, remainder is yellow. Tibia and basi tarsus yellow. Tibia about .7 as long as the basi tarsus. Remainder of tarsus appears dark because of presence of setulæ. Coxa of mesothoracic leg yellow except for brown band on the outer anterior surface and a narrow black stripe at the distal portion. Trochanter yellow. Femur with a narrow brown band at the base, the remainder yellow. Tibia and tarsi yellow but covered with black setulæ. Coxa of metathoracic leg resembles that of the mesothoracic leg except that the brown area is larger. The rest of the leg is the same in appearance as the mesothoracic appendage.

Abdomen. Dorsum of segment one entirely dark brown. Segments two through five have the dorsum dark brown except for a posterior lateral yellow spot on either side. Ventral portion of abdomen yellow. Hypopygium dark brown, resembles somewhat that of *Ceroplatus militaris* Johannsen. It can be distinguished from that of Johannsen's species by the lack of dense clusters of black setae on the inner and dorsal surfaces of the base of the disti-style.

This new species would run to *Ceroplatus militaris* in Johannsen's key. It can be distinguished from *militaris* by the structure of the hypopygium, as already discussed; by the relative lengths of the fused portion of veins M and R and the petiole of media; and by the markings.

Described from one male taken in September 1940, at Fernald Hall, Massachusetts State College, Amherst, Massachusetts by Dr. C. P. Alexander. Type in my collection.

A NOTE ON *HIPPOBOSCA MARTINAGLIA* BEDFORD (DIPTERA, HIPPOBOSCIDÆ)

By J. Bequaert

Harvard Medical School and School of Public Health, Boston, Mass.

In my second revision of the Hippoboscidæ (1939, Psyche XLVI, pp. 70-90), I accepted *Hippobosca martinaglia* Bedford (1939) as a valid species on the basis of the original description and figure. Shortly before his death, the late Dr. G. A. H. Bedford promised to send me a paratype, but unfortunately he was never able to do so. Dr. R. du Toit, Veterinary Research Officer at Onderstepoort, has since gone to considerable trouble in order to clear up the identity of this parasite. It was not possible thus far to trace Bedford's types, which are either mislaid or lost. In July, 1940, Dr. du Toit was, however, able to obtain specimens of a *Hippobosca* collected on the type host (Impalla, *Æpyceros melampus*) at the type locality (Bar R Ranch, Swaziland) of *H. martinaglia*. The male and female, which he sent me of this lot, agree well with Bedford's description and they are obviously his species. At the same time it is impossible to separate them from *Hippobosca fulva* Austen. Bedford's *H. martinaglia* I regard therefore as a synonym of *H. fulva*. The name *martinaglia* should be removed from the list of valid species of *Hippobosca*, which now number eight only. In the key of my 1939 paper couplet 6 should be discarded, the second alternative of couplet 5 running directly to couplet 7.

The wing of *H. martinaglia* is exactly like that of *H. fulva*, the second longitudinal vein being about as long as the apical section of the third longitudinal (Bedford's figure is incorrect in this respect), and the basal section of the third longitudinal vein is bare. There is only one pair of vertical bristles on the head. The scutellum bears nine preäpical

bristles in the one female seen and eight in the one male. The arrangement of the tergal sclerotized plates of the abdomen is, in the male, similar to that of the males of *H. equina* and *H. longipennis*, but the first (anterior) two median tergal plates are very small. In the female I can find no trace of a third median tergal plate, the second is small and the first barely indicated (Bedford's figure, drawn from the female, does not show the median tergal plates). The color-pattern, although fairly correctly outlined by Bedford, is by no means as boldly marked as in his figure; it agrees, moreover, with that of other specimens of *H. fulva* seen.

Dr. du Toit also sent me a male of *Hippobosca fulva*, taken by Mr. Alex. Cuthbertson from a purple-crested lourie or plantain-eater (*Gallirex p. porphyrolophus* Vigors) on the Sabi River, eastern Transvaal. The host was no doubt accidental.

I may emphasize, on this occasion, that color and markings are, as a rule, without value as specific characters in Hippoboscidae, a fact not fully recognized as yet by some recent authors. Not only do they vary individually within the same species, but they often change in the same specimen. During life, such color changes may be due to age (time elapsed since hatching), to the fed or unfed condition, to parturation (in females), or to the nature of the diet and other environmental factors conditioned by the host. After death, the color of the living insect may be more or less modified by the method of killing and preservation, as well as by the length of time the specimen was kept in collections.

THE SUMATRAN "TRILOBITE LARVA"

By Charles T. Brues

Biological Laboratories, Harvard University

The appellation of "Trilobite Larva" has been in use for many years to designate the larvæ of certain highly aberrant malacoderm beetles. These attain a length of one to several inches, with wide, greatly flattened body. The three thoracic segments are expanded laterally forming a sort of carapace and the abdominal segments bear long, curved projections. These gross characters give the larvæ an almost comical, but nevertheless extraordinarily striking resemblance to certain long-extinct trilobites.

The first reference to these larvæ appears to be that of Perty made over a century ago, in 1831. His account relates to a form from Java which Westwood figured in his "Modern Classification of Insects"[1] a few years later. With his usual taxonomic acumen, Westwood suspected that this larva belonged to some species of the family Lycidæ. Since that time a number of additional species have been discovered in various parts of the Indomalayan region to which they they are apparently restricted. They seem to be best represented in Borneo where at least six distinct types have been discovered. These have been dealt with at length by Mjöberg in 1925[2] who gives an historical and descriptive account that need not be repeated here. Mjöberg was successful in rearing one Bornean species to maturity and found that the large larvæ are females which are destined to undergo practically no external change on becoming adult. Unfortunately he overlooked a paper by the Dutch naturalist, J. C. Koningsberger[3] published more than twenty years pre-

[1]Vol. 1, p. 254; fig. 27, 1-2 (1839).

[2]The Mystery of the so-called "Trilobite Larvæ" definitely Solved. Psyche, vol. 32, pp. 119-153, 2 pls.

[3]Een Geheimzinnige Larve. De tropische Natuur, Jaarg. 1, pp. 17-20 (1912).

viously where the transformation of the common Javan species was accurately described. Koningsberger observed the molting of the large larvæ into larviform adults and proved them to be sexually mature females as several of his specimens deposited perfectly formed, though infertile, eggs. Koningsberger was disappointed not to secure the male which was discovered first by Mjöberg. The latter is a small lycid beetle, quite similar to the other members of the family Lycidæ and scarcely one-tenth the length of the huge larviform female. The larval form of the male has never been discovered; in fact no very small larvæ have ever been recorded and Mjöberg found only large ones obviously greatly in excess of the size which the male would attain before transformation into such a small adult. On this account he supposed that the larvæ must be sexually dimorphic, but this supposition does not necessarily follow although it must be admitted that the female forms are extraordinarily aberrant while the adult male is a perfectly normal beetle.

The species here illustrated is from the highlands of southern Sumatra, near the town of Pagaralam, in the edge of a jungle close to a waterfall a few kilometers out of the town at an altitude of about 3–400 feet. My wife and I had stopped to collect near the waterfall and she discovered two specimens beneath some loose rotted wood lying in an open area. We immediately instituted a search for further examples in the neighborhood, but without success.

A comparison of the two larvæ reveals that they are very different from any of the Bornean forms described and illustrated by Mjöberg. They resemble closely, however, one collected somewhere in the Malay peninsula illustrated by him. This specimen is in the Kuala Lumpur Museum, but no locality is mentioned and presumably its exact provenience is not known.

When I first examined the two Sumatran specimens, it seemed that they must be identical with the Javan one as they agree well with Westwood's figures and the description given by Perty. Furthermore, a cursory examination of specimens from Java which I saw later in the Buitenzorg Museum revealed no obvious differences and Mjöberg refers a specimen collected near Pematangsiantar, Sumatra to the

original Javan species. Several earlier records of such larvæ from Sumatra also assume they are identical with the Javan one. There are, however, in the Museum of Comparative Zoology four specimens from Java[4] and closer scrutiny shows the Sumatran species to be quite distinct. It is evidently widely distributed as our specimens are from southern Sumatra and Mjöberg found it in the northern part of the island, strangely enough in a region where we failed to discover it although we spent some weeks in the jungle near Pematangsiantar. Kolbe in 1887 recorded its occurrence at Penang on the west coast.

In the collection of the Museum of Comparative Zoology there are a number of other trilobite larvæ one of which appears to represent a species that has never been described or figured and I am appending at the end of the present note a description of this as well as the Sumatran one together with the morphological characters that may be used to distinguish the several species that are available to me. The species are all readily recognizable by good taxonomic characters and these may be applied to the diagnosis of other species as they may come to the notice of entomologists.

The Sumatran Species

(Plate 2; Text–fig. 1)

Attaining a length of at least 37 mm. Color dark brown, but fading considerably in alcohol; the tubercles on the dorsal thoracic and abdominal segments shining black, the underside likewise brown, with the abdomen blackish at the sides and apex; the legs blackened apically. The lateral abdominal projections with yellowish tips, the pale color extending further basad on the apical segments, the last segment entirely pale both above and below. Thoracic segments rather wide and short, the mesothoracic dorsum almost two and one-half times as wide as long. The shining black tubercles or warts well developed, one on each side of the pronotum; a pair similarly placed on the meso– and the metanotum and all three segments with a pair of minute

[4]One from "Java" (Professor Roland Thaxter) and three from Bantar Gelbary (Bryant and Palmer).

ones at the posterior margin near the middle; abdominal tubercles very small, transverse, arranged in pairs near the middle of the hind margin of each of the basal six tergites, but these are lacking on the last three tergites. Lateral horns or processes on the abdomen long; except the first, all are curved backwards, but not upwards; those of the

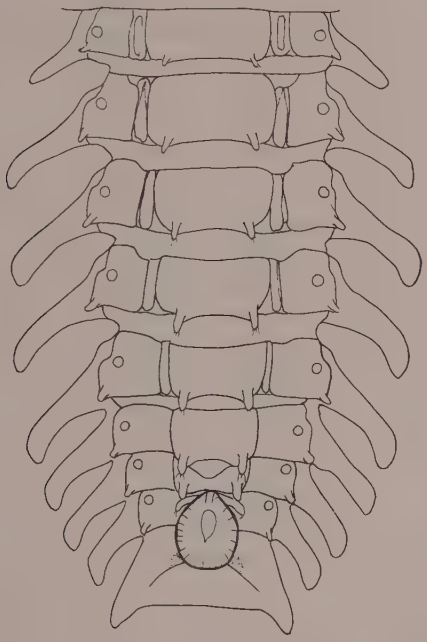

Fig. 1. Ventral view of abdomen of Sumatran "Trilobite" larva.

last tergite short, simply extending its lateral angles; those of the first short and pointed at tip, the others blunt. On the underside the meso– and metasternum each bear a minute, convex tubercle at the center. Each abdominal sternite with a tooth-like projection on each side at the posterior angle. Each of the pleurites, which lie directly below the lateral processes of the terga, is produced at the posterior angle into a blunt tooth and each is perforated by a deep, circular, spiracular opening. The two spiracles of the thorax are similar and lie at the anterior margin of the meso– and

metathorax, just inside the lateral shelf-like extensions of these segments. Dorsally the anterior margin of these is sharply truncate with a slight, rounded tubercle at each side and a pair of more pronounced ones medially, separated by a slight median emargination.

In its general habitus this species is very similar to one illustrated by Mjöberg from the Malay Peninsula, but his photograph is not sufficiently clear to indicate this definitely, and other accounts of what may be the same species are likewise lacking in details.

The Javan Species[5]

(Plate 2)

The four specimens of this form are all smaller than the preceding species as the largest one does not exceed 30 mm. in length. The color is darker, but this is quite probably due to the preservation. The thorax is fuscous above or darker and the abdomen piceous or nearly black, with the lateral projections orange yellow on the apical half. Structurally, the differences are as follows. The larger, posterior tubercles of the meso– and metathorax are more strongly transverse; the posterior margin of the metanotum bears four small warts, the additional ones more minute than the median pair and forming with them an equidistant series of four. The abdominal warts are present on the seventh and eighth segments so that there are eight instead of six pairs. The thorax is wider, the mesonotum measuring nearly three times as wide as long. The lateral abdominal projections are stouter, more swollen apically and quite evenly rounded at the apex.

One specimen bears the label "Java, R. Thaxter". The others, collected by Bryant and Palmer, are from Bantar Gelbary.

A Bornean Species

(Plate 3)

A series of specimens from Sadong, Sarawak, Borneo collected by Harrison Smith are apparently the form figured

[5]Burgeois, (Bull. Entom. Soc. France, 1899, p. 61) has given a description of this form, but not having the Sumatran one for comparison does not refer to the differential characters.

by Mjöberg as "No. 5" which he speaks of as the common lowland type in this portion of Borneo. It is much lighter in color, being a uniform light brown with the dorsal protuberances and warts greatly reduced. The pronotum and abdominal tergites lack the warts completely and those of the meso– and metanotum are reduced to a single elongate, streak-like, smooth elevation midway between the median line and lateral margin, longer on the metanotum. The mesonotum is very wide, fully three times as broad as long and the metanotum is produced at each side into a very long, obtuse lobe. The lateral projections on the abdominal segments are very long, curved evenly upwards and backwards and evenly attenuated from the base to the tip, with the basal one as usual much shorter. The anterior margin of the pronotum bears four prominent rounded or more or less tooth-like tubercles or projections separated by conspicuous emarginations. The specimens range in size to fully 45 mm.

A description undoubtely of this form has been given by Bourgeois[6] and the preceding paragraph refers mainly to characters of use in differentiating it from other species.

Captain Barnard's Larva

(Plate 3)

This is a very striking form, similar in habitus to the Bornean species of which Mjöberg reared the female and later secured the male, *Duliticola paradoxa* Mjöb.[7] It differs at once, however, in the presence of large shining tubercles on the disk of the three thoracic segments. The arrangement and size of these raised areas are the same as in the Sumatran species as are also the minute warts on the posterior margin of these segments, except that the latter are very minute. The mesonotum is slightly more than twice as wide as long. The abdominal tergites bear also pairs of minute warts at the posterior margins; these are very distinct, becoming smaller on each succeeding tergite and not visible at all beyond the fifth. The lateral processes of the abdomen are very strongly curved upwards and posteriorly,

[6]Bull. Entom. Soc. France, 1899, p. 59.

[7]This is apparently the form described at length, but not named by Hanitsch in 1900 (Journ. Roy. Asiatic Soc., Straits Br. No. 34, p. 78).

almost hooked at their obtusely rounded tips. The entire larva is piceous or black, about 50 mm. in length.

The exact provenience of this specimen is unknown. It has been in the Museum of Comparative Zoology for over 60 years and bears the label "J. Barnard, East Indian Ship 'Monsoon' ". I have figured it as it adds still another species to the considerable number already known.

Explanation of Plates

Plate 2

Upper two figures, Sumatran "trilobite" Larva.
Lower two figures, Javan "Trilobite" Larva.

Plate 3

Upper two figures, Bornean "Trilobite" Larva.
Lower two figures, Barnard's "Trilobite" Larva.

PSYCHE, 1941 VOL. 48, PLATE II.

Brues — "Trilobite Larvæ"

PSYCHE, 1941 VOL. 48, PLATE III.

Brues — "Trilobite" Larvæ

A NEW CUBAN MILLIPED, WITH NOTES AND DRAWINGS OF OTHER WEST INDIAN SPECIES

By H. F. Loomis

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In June, 1940, the writer visited the Museum of Comparative Zoology, Cambridge, Massachusetts, to examine certain type and other specimens of millipeds in the collection there. In the material seen was a recently received Cuban species of *Amphelictogon*, obviously differing from other known members of the genus. A description of this species follows.

Also the opportunity is taken for presenting drawings made from a number of R. V. Chamberlin's types of West Indian millipeds, especially those in the genus *Amphelictogon*, where the difficulty of distinguishing the species without reference to illustrations of the gonopods has been found very great or, in certain cases, impossible.

A species described by C. H. Bollman which, for over 50 years, has erroneously reposed in the family Platyrhacidæ is here transferred to another family where a new generic name is proposed to admit it.

Amphelictogon cubanus Chamberlin

Bull. Mus. Comp. Zool., vol. 52, No. 5, p. 224, 1918.

This is the only known member of the genus having the dorsal surface of its segments divided into definite quadrate or polygonal areas. A gonopod of the type is shown in figure *d* of the plate.

Amphelictogon bahamiensis Chamberlin

Bull. Mus. Comp. Zool., vol. 52, No. 5, p. 231, 1918.

The type and only known specimen of this species is

approximately 15 mm. long. One of its gonopods is shown in figure *b* of the plate.

Amphelictogon rex sp. nov.

In the Museum of Comparative Zoology collection are three males, including the type, collected in the Sierra de Nipe, Cayo del Rey, Oriente Province, Cuba, April 1940, by J. P. Carabia.

Diagnosis: This species belongs in the series with color differences between the poriferous and non-poriferous segments. Its closest relatives appear to be *A. obscurus* Chamberlin and *A. bidens* Loomis but with obvious differences from them in coloration and modifications of the gonopods.

Description: Length 30 mm.; width 4.5 mm. across posterior margins of segments 1 and 2; 4 mm. across the middle of the body which is parallel-sided to about segment 15, after which it narrows to the last segment.

In alcohol the head is dark brown except for the narrow white anterior margin; antennæ with basal joints light colored, the outer joints dark brown; legs and ventral surface of all segments white; segments 1 to 4 dark brownish-black except the pure white posterior corners; poriferous segments from the fifth to the penultimate have the prozonites brown with a large white spot in front of the keels, reaching nearly to the middle of the dorsum; metazonites with the keels and sides of the dorsum white, only the median line dark brown; non-poriferous segments have the sides and dorsum of the prozonites dark brown metazonites dark brown, except the outer two-thirds of the keels, which are white; last segment brown at base, white at apex.

Surface of segments shining, the keels with two or three small granules, each with a tiny pit at middle from which a seta may once have projected; segments 2 to 8 with a tooth at the anterior corner of each keel; posterior margin of most keels from segment 5 to segment 16 with two teeth, the outer of which is largest; margins of poriferous keels raised above the inner surface of the keel, the elevation most evident at the rounded anterior corner; pore callus elongate, formed by the gradual thickening of the margin, the pore opening obliquely outward and upward.

Preanal scale rather thick, broadly rounded behind, with a tiny supplementary projection at middle of posterior margin.

Gonopod as shown in figure *a* of the plate.

Sternum between the third legs narrow, high, almost hemispherical and with a considerable number of erect setae; sterna between the fourth and fifth legs higher and with more erect setae than the third sternum.

Schizodira gen. nov.

Type *Stenonia maculata* Bollman, Proc. U. S. Nat. Mus., Vol. 11, p. 336, 1888.

Syn. *Platyrachus? maculatus* (Bollman) Chamberlin, Bull. Mus. Comp. Zool., Vol. 62, No. 5, p. 216, 1918.

Review of the original description convinces me that this species cannot possibly belong in the Platyrhacidae where Bollman and subsequent writers placed it. Bollman compared *maculata* with *Stenonia fimbriata* (Peters) but it appears that either he never had seen Peters' species or he misinterpreted the original description of it, for it is certain that *fimbriata,* made the genotype of *Tirodesmus* by Cook in Brandtia, p. 51, 1896, is not related generically, at least, to *maculata.*

I know of no species of Platyrhacidæ as small as *maculata,* and none of this family has an expanded, crenate, front margin on the first segment, completely hiding the head from above, nor does the body have a pronounced longitudinal median line. These characters, however, are found in the Chytodesmidæ and Stiodesmidæ but in the description of *maculata* there is given no character indicating in which of these families it should be placed. Nevertheless, Bollman's inclusion of it in the genus *Stenonia,* which he later distinguished in two keys on the position of the pores, allows the inference that the pores of *maculata* are on the dorsal surface, removed from the lateral margin of the keels, a character placing the species in the Chytodesmidæ, rather than in the Stiodesmidæ which has pores on special processes of the margins of the keels. As no other chytodesmid genus has a notch between the third and fourth crenation from the posterior corner of the first segment, the generic

name, *Schizodira*, in reference to this character, is proposed for combination with *maculata*. Other diagnostic characters may be found in Bollman's statement "lateral carinae crenulate, the first six, the eighth, eleventh and fourteenth, with two crenulations, the rest with three," although it is probable that he actually meant segments 2–6, 8, 11 and 14, as segment 1 had previously been described as having 12 crenations. The pores apparently were in the normal sequence on segments 5, 7, 9, 10, 12, 13, 15–19.

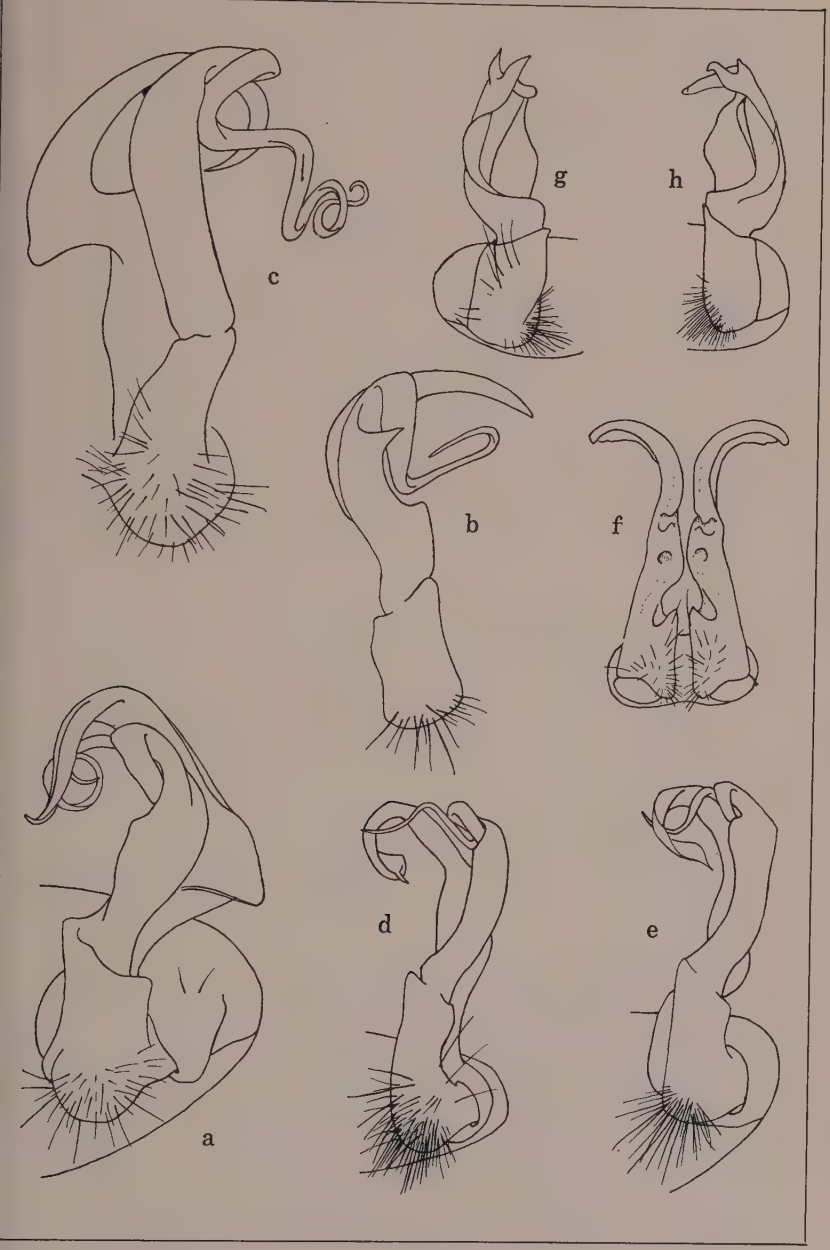
This species has not been rediscovered since Bollman's time and several hasty searches through the disorganized milliped collection of the U. S. National Museum have failed to reveal the specimens Bollman deposited there.

Explanation of Plate 4

a, *Amphelictogon rex*: Gonopod; b, *Amphelictogon bahamiensis* Chamberlin, Gonopod; c, *Amphelictogon pallidipes* Chamberlin, Gonopod; d, *Amphelictogon cubanus* Chamberlin, Gonopod; e, *Amphelictogon rubripes* Chamberlin, Gonopod; f, *Caraibodesmus bruesi* Chamberlin, Gonopod; g, *Cubodesmus ramsdeni* Chamberlin, Gonopod; h, *Cubodesmus pelopleurus* Chamberlin, Gonopod.

All drawings made from type specimens.

PSYCHE, 1941 VOL. 48, PLATE IV.



Loomis — West Indian Millipeds

CHARACTERISTICS OF THE LARVIFORM FEMALE OF THE LAMPYRID BEETLE, LAMPROPHORUS

By Charles T. Brues,

Biological Laboratories, Harvard University

In looking over the collection of larvæ of malacoderm beetles in the Museum of Comparative Zoology searching for specimens of the remarkable Lycidæ commonly known as "trilobite larvæ", I noted two specimens from Ceylon that represent the larva and larviform adult female of a species of Lamprophorus. The label indicates that these were received from F. Layard in January, 1865. Like the other known members of the genus the female larva attains a large size which corresponds to that of the adult female, in this case about 70 mm.

An early reference to these larviform lampyrids is a note on page xlviii the Proceedings of the London Entomological Society for 1908 that mentions the exhibition by C. J. Gahan of specimens of Lamprophorus (*Lamprigera*) and Dioptoma and sets forth briefly the slight differences that distinguish the sexually mature female from the larva. In the same journal for 1912 (p. 178) Green gives a very brief description of the "grub-like" female of *Dioptoma adamsi* Pasc. with an account of the luminous organs which are present in both sexes. Dioptoma is now placed in the related family Rhagophthalmidæ although Lamprophorus is still retained in the Lampyridæ.

Blair[1] has described a larva, probably of *Lamprophorus boyei* Mots. from Sumatra. These larvæ were collected together with the male of this species at two localities. In the same paper he records the female of *L. tenebrosus Walk.* from Ceylon, definitely identified as it was taken *in coitu* with the male. He notes that it is of very similar form to the larva, "but of pale colour with more feebly chitinized in-

[1]Journ. Fed. Malay States Mus., vol. 8, p. 176 (1928).

tegument; the antennæ are of similar form except that the third joint has become more elongate and divided into five small joints, the mouthparts differ in numerous particulars and the legs have a 5-jointed tarsus." In this same paper Blair gives a rather detailed description of the Sumatran larva, especially of the mouthparts and antennæ, but no further details are included concerning the more minute structures in which the female differs from the mature larva.

I have undertaken to do this for the two specimens before me as the matter is of considerable interest for it illustrates the great persistence of certain morphological characters in insects even when an almost complete degeneration of most bodily structures supervenes for one reason or another. In the great majority of cases among insects, or other animals, such great degenerative modifications or simplifications are directly traceable to parasitic life such as those shown, for example, by female Strepsiptera, parasitic earwigs and the like. Such is, of course, obviously not the case among the Lampyridæ where numerous other examples of larviform adults are well known. These occur in more than one series of related forms, at least one of which, Phengodes, is often relegated to another family and in the family Lycidæ where a closely similar condition exists in some Indomalayan genera. In the latter, as in Lamprophorous and its allies, a remarkable disparity in size between the sexes develops as the female becomes a ponderous creature in comparison with her diminutive, though normally proportioned spouse.

The fully grown larva and adult female of Lamprophorus are of essentially the same size and general proportions. The larva is not particularly extaordinary for a Lampyrid and the structure of the head with its appendages and the legs are of normal form.

The female differs most noticeably in its paler color and much more delicate integument which is far more flexible and apparently thinner. Ecdysis is complete as there is no indication of any bits or shreds of the larval cuticle still adhering to the surface of the body such as have been described by Mjöberg for one of the lycid "trilobite" larvæ which he reared to maturity. The head in dorsal view is much narrower behind than in the larva, but otherwise the dorsal segments are essentially similar in shape and even

retain evidences of a rather complicated pattern of surface sculpture, indicating that aside from molting the pigmented layer of the cuticle, no metamorphic change in the integument takes place. The legs of the larva (Fig. 1,C) are of the usual form, with three joints and a single, simple claw. The leg of the adult female (Fig. 1,F) is a true imaginal structure with the coxa, trochanter, femur and tibia developed in more or less normal proportions and there is a five-jointed tarsus bearing two large, dentate claws.

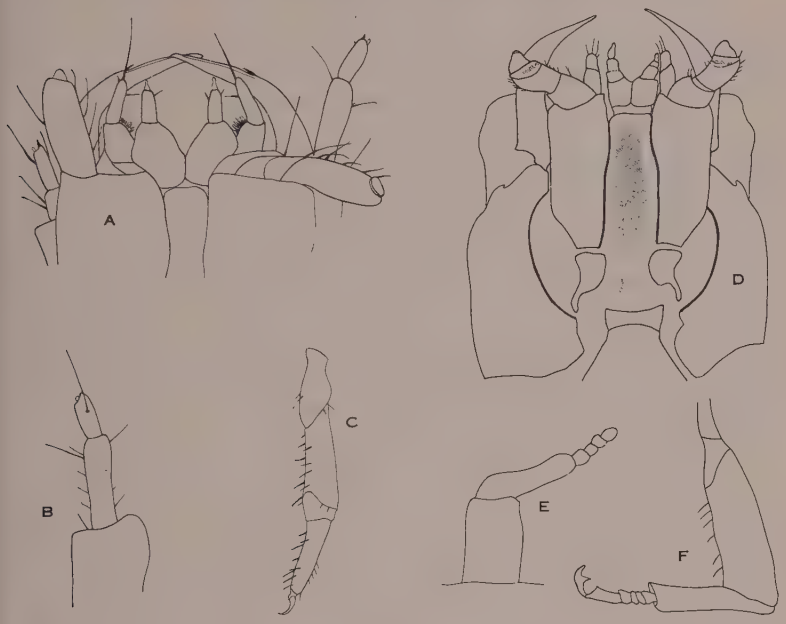


Fig. 1. Lamprophorus sp., details of larva and adult female. A, head of larva from below; B, antenna of larva; C, leg of larva; D, head of female from below; E, antenna of female; F, front leg of female.

The antennæ (Fig. 1,E) are but little longer than in the larva, but are clearly six-jointed. In this connection it is of interest to note that the males of Lamprophorus exhibit a shortening of the antennæ through the disappearance of several apical joints and shortening of the basal ones.

The presence of numerous spheroidal eggs about three

our four millimeters in diameter proves that the specimen is fully mature.

Several changes in the mouthparts occur at the final ecdysis (Fig. 1; A, D). The large, pointed, falcate mandibles of the larva are tapered to a point and bear a conspicuous groove externally on their apical third. Those of the adult have the apex flattened into an obliquely truncate edge which lies in a vertical plane so that the tip appears acute in ventral view and only close observation indicates that the mandibles undergo a quite considerable change in shape. The maxillary palpi are obviously shortened in the adult, but the actual changes are slight. The maxillæ themselves are also shorter in the adult. The labium is changed mainly by the addition of another joint in the palpi. All of these changes in the mouthparts clearly represent a degeneration in functional capacity but they include also the retention to some slight degree of features involved in the increased complexity that normally characterizes the imaginal stage. The same is also true of the tarsi and this is of particular interest, since the segmentation of the tarsi is one of the most remarkably constant characters, among practically all groups of insects, and it is only slightly changed in the female Lamprophorus despite the inhibition of so many of the more conspicuous imaginal features and the absolutely larviform habitus.

The accompanying figures drawn for me by Mrs. A. S. O'Connor illustrate the several structures to which reference is made.

SOME FLIES OF THE FAMILY SYRPHIDAE, MESOGRAMMA

By Frank M. Hull

University of Mississippi

This paper describes some new species of Syrphidae from the Neotropical region, derived from various sources. Types are in the author's collection unless otherwise stated.

Mesogramma vitrea n. sp.

Male. Length 5 mm.. *Head:* face and front and antennæ light, pale yellow, the cheeks black, the vertex golden brown, becoming coppery just behind the ocelli. Occiput metallic brassy above, greyish white along the sides. *Thorax:* metallic brassy brown with a prominent median steel blue stripe on either side of which are two dark brown and two light brown stripes. Pleuræ shining metallic, with a small obscure yellow spot on the upper part of the sternopleuræ and the posterior margin of the mesopleuræ. Scutellum and humeri metallic brassy black. *Abdomen:* highly polished and shiny, first three segments wholly black, last two segments dark shining reddish brown. Hypopygium shining black. Pile of abdomen abundant, rather long, whitish upon the margins and lateral portions of all of the segments and blackish upon a central stripe down the middle of the abdomen which begins upon the posterior part of the second segment. *Legs:* chiefly shining black, the tips of the femora, the tips of the hind tibiæ and its base yellow. Hind basi-tarsi and the three terminal joints dark brownish black. Middle of the fore and mid-tibiæ with an obscure brownish band. Anterior tarsi darkened. *Wings:* pale brownish.

Holotype male. São Paulo, Juquia, J. Lane, Nov. 7.

Mesogramma picta Sch. variety **melleoguttata** n. var.

Female. Length 6 mm. *Head:* vertex violet, front shining metallic black, its narrow sides and the face pale yellow,

cheeks black, occiput brassy brown above, becoming yellowish grey on the sides and below. Antennæ brownish, the ventral portion reddish orange. Arista brownish black, the antennal pile black. *Thorax*: with a broad median bluish grey shining vittæ, and lying outside of it, first a pair of dark brown vittæ, then a pair of somewhat yellowish vittæ, and bordering the continuous yellow side markings are a pair of wide brown vittæ. Pleuræ yellow on the posterior margin of the mesopleuræ and upper part of sternopleuræ. Scutellum metallic black, the margin pale yellow. *Abdomen*: black marked with light yellow, sides of the first segment and its narrow margin, a complete transverse stripe on the second segment that reaches the sides, its anterior corners narrowly, and traces of a median vittæ, all yellow. Third segment with a median yellow vittæ which does not quite reach the posterior margin and on either side of it two basal yellow spots. The outermost pair subrectangular, occupying the corners and narrowly confluent at the base with the submedial much larger spots which are twice as long as the more lateral ones. The submedial spot on inner surface is strongly indented and the black encroaches upon it, but only upon the basal half of its medial surface. Fourth segment with almost identically similar pattern. Fifth segment with large yellow spots on the basal corners and a pair of widely separated elongate, yellow spots broadly reaching the base of the segment with the posterior ends rounded and very slightly approximated. *Legs*: pale yellow, the hind tarsi, basal two-thirds of hind tibiæ and a wide black annulus apically upon the hind femora, black. *Wings*: pale grey, stigma pale brown.

Holotype female. Barro Colorado Island, Canal Zone, Aug. 25, 1937. Hull coll.

Mesogramma elongata n. sp.

Male. Length 13 mm. *Head*: face and front yellow, the antennæ brownish yellow, third joint slightly darker dorsally, cheeks shining blackish, upper part of vertex brilliant violet, giving way to steel blue just behind the ocelli, area between the ocelli golden brown, lower part of the frontal triangle greyish pubescent. Occiput yellowish grey pubescent. *Thorax*: mesonotum with a broad bluish grey median stripe divided posteriorly by a narrow steel stripe the greater

part of the mesonotum outside of the stripe golden brown. Between the golden brown and the lateral yellow margins is another metallic grey stripe. Humeri posterior two-thirds of the mesopleuræ and a spot on the upper part of the sternopleuræ pale yellow. Suctellum pale yellow, the disc broadly metallic brown. *Abdomen:* black marked with yellow, first segment about half black, the anterior part yellow including the lateral margin which is narrowly continuous with the lateral margin of the second segment. Second segment shining black, with an extensive transverse yellow band from margin to margin which is in width barely over one-fifth the length of the segment. Third segment broadly black upon the posterior part; about one third of the way from the end of the segment it sends forward a broad vittæ that rapidly expands into a large black spot, the anterior pointed end of which reaches the base of the segment. From the base of this median vittæ at its posterior point of origin, the black extends obliquely forward to the lateral margin of the segment and thence forward to occupy almost all of the lateral margin of the segment. At its lateral marginal apex it is confluent with a small oval black spot situated anteromedially, which small spot is narrowly separated from the large median subbasal spot. Fourth segment with similar pattern but the apex of the segment and lateral margins of the segment are extensively reddish brown and the somewhat smaller sublateral, subbasal black spots are more slender, more pointed and isolated. There is a fine narrow median reddish brown line bisecting the middle black vitta. Fifth segment with a pair of obtusely triangular submedial brown spots and lying just outside of these, touching the base are a pair of elongate brown vittate spots hollowed out on the inside, on the posterior two-thirds of their length. *Legs:* pale yellow, a brownish band subapically on the hind femur almost the whole of the basal half of the hind tibiæ and all of the hind tarsi, fore and middle tarsi brownish. Hind femora with considerable, rather long, black, bristly pile ventrally. *Wings:* hyaline, stigma dark brown.

Three males. Cotypes; Muzo, Department Boyaca, Columbia, altitude 900 meters, 1936. J. Bequært col. A specimen deposited in the Museum of Comparative Zoology.

Salpingogaster pessulagyna n. sp.

Male. Length 13 mm. *Head:* face, cheeks and front pale yellow, the latter with a brownish black longitudinal spot. Antennæ wholly light orange, its pile dark brown. Vertex blackish. *Thorax:* with a pair of prominent, narrowly separated, golden pollinose vittæ. On either side of these are an additional pair of somewhat less conspicuous golden vittæ; these outer vittæ are bordered by blackish brown. Humeri, most of the notopleuræ, post calli and a confluent spot anterior to them, the wide posterior margin of the scutellum, a transverse fascia upon its base all pale yellow. All of the pleuræ pale yellow except a narrow, oblique, brown band and a darker brown spot anterior to the halteres. Greater discal part of the scutellum and the metanotum brownish black. *Abdomen:* chiefly light reddish brown without black markings. The first segment pale yellow, its posterior margin with a brown fascia which, however, does not reach the base on either side. Fifth segment brownish yellow. Hypopygium pointed, last sternite with a pair of prominent black setate nodulose projections. *Legs:* light yellow, the middle and posterior femora narrowly yellowish brown subapically. Femoral setæ brown. *Wings:* pale brown with a well developed anterior brown margin reaching to the end of the wing, the costal cell paler.

Holotype: male. Barro Colorado, Aug. 28, 1938 (F. M. Hull, collector).

Fazia hermosa n. sp.

Male. Length 10 mm. *Head:* face and lower part of occiput and the wide ocular margin of the front pale yellow. The pile abundant, long, erect and black. A broad black stripe running down the middle of the face enclosing the small but prominent tubercle. Front with a transverse, black spot above the widely separated antennæ, the spot continuing narrowly to the point of contact with the eyes. Epistoma standing out a little way beyond the base of the antennæ. Antennæ dark reddish brown, blackish along the dorsal third of the third joint. Mesonotum dull brownish black with a brassy cast, very feebly shining the humeri dark. There is a large, conspicuous, triangular, yellowish, noto-

pleural spot that is confluent with a broad, post-marginal stripe of the mesopleuræ and an obscure spot on the upper spot of the sternopleuræ. Post calli and the scutellum light yellow, the latter with a diffuse, though conspicuous, black discal spot. Pile of thorax and pleuræ thick, erect and reddish brown, becoming longer and blacker on the scutellum. *Abdomen:* with nearly parallel sides, widest at the base of the fourth segment, where it is fully as wide as the widest part of the thorax. Abdomen nearly opaque black with five pairs of yellow spots, none of which, except the first pair on the first segment, reach the lateral margin. Spots on the first the segment. Third segment with more elongate spots, separated by less than the width of a spot. The spots of the fourth segment practically identical with the third; the spots rated by at least the length of a spot. The spots are roughly triangular, with rounded angles, and placed midway along the segment. Tihrd segment with more elongate spots, separated by less than the width of a soot. The spots of the fourth segment practically identical with the third; the spots of the fifth segment somewhat smaller, with sharply-pointed inner ends and more narrowly separated. Pile on the basal part of the abdomen reddish-brown, becoming almost yellow on the extreme corners, elsewhere black. *Legs:* chiefly black; base of the hind femora, their apices and the apices of the middle femora, front femora and the bases of their respective tibiæ dark brownish. *Wings:* with a strong brownish uniform tinge. Subapical cross vein elongate, the final section recurrent, the entire cross vein sigmoid.

Holotype: male. São Paulo, May 6-8, 1939 (J. Lane, collector).

THE ANTIQUITY OF SOCIAL INSECTS

By J. C. Bequaert and F. M. Carpenter
Harvard University, Cambridge, Mass.

The geological antiquity of social habits among the insects has been the subject of much speculation. Estimates of the time of origin of social insects show little agreement and range from the Permian to the Eocene. Up to the present time, however, actual remains of insects belonging to social families have not been found in strata older than the Eocene. For this reason the Cretaceous fossil recently described by Dr. R. W. Brown[1] as *Celliforma favosites* is of much entomological interest. In Dr. Brown's opinion this specimen represents the comb of a wasp nest and thus constitutes the earliest geological record of the social wasps and of social insects in general. Through the kindness of Dr. Brown, we have been able to examine the fossil itself and to discuss it with our associates. We are convinced from this examination that Dr. Brown's identification of the fossil is a doubtful one, and are of the opinion that it is not the nest of a social wasp. If this fossil were from a Tertiary deposit, it would have relatively little significance; but being from the Cretaceous, it would, if unquestionably identified, greatly extend the range of the social wasps. Because of this, we have decided to publish a discussion of the fossil and of our reasons for the above conclusion. The antiquity of social habits among the insects is a very complicated question, as we shall indicate later, and all suggestions deserve serious consideration; but we believe that evidence bearing on the subject should be critically and carefully examined before definite conclusions are reached.

The piece of rock containing the fossil is an irregular ironstone nodule, the center of which is occupied by the fossil. One half of the specimen (shown on plate 1 of Dr.

[1]Amer. Journ. Sci., vol. 239, January, 1941, pp. 54-56.

Brown's paper) shows a series of dome-shaped projections, arranged in rows; these are regarded by Dr. Brown as casts of the cells of the nest.[2] The counterpart of the fossil is lined by shallow cavities which fit over the ends of the projections. One portion of this counterpart also has projections like those on the other half, so that when the parts of the concretion are placed together, the dome-shaped projections extend inwards from both sides. This extraordinary condition, which is not mentioned by Dr. Brown, seems to require an explanation, if the specimen is regarded as a nest.

The method by which a wasp nest might be preserved so as to resemble the fossil in question is very difficult to imagine. Dr. Brown has concluded that the specimen represents part of a papery nest like that of *Polistes*, but he was apparently unable to explain to his own satisfaction the process of preservation, for he left "to the reader the pleasure of speculating as to the circumstances and method by which the original comb became this fossil." It seems clear that in order to have a nest so preserved, particles of sand and mud must have filled the cells and become cemented together while the walls retained their shape. Then, since there is no part of the actual nest remaining, its substance must have been replaced by additional sand and mud, as it disintegrated. In this way a cast of the nest or of a portion of it would be formed. This process of preservation, involving two steps, seems to be inevitable, and it is indicated by the lithology of the fossil, for the sand particles forming the casts of the "cells" differ in size and other details from those replacing the "cell" walls. What seems impossible to us is that the paper nest would retain its shape long enough to allow the filling in the cells to become so hard that it would hold its form after the disintegration of the paper walls. If a paper comb of any living genera of social wasps (i.e., Vespinæ, Polybiinæ, Polistinæ, Ropalidiinæ) were buried and filled with sand and mud, the thin soft walls between the cells would, in our opinion, inevitably disappear within a short time, long before the foreign material could harden. We have not, of course, experimented with a nest to determine how long it could hold its shape under such conditions;

[2]Dr. Brown refers to the fossil as a *mould*, but we consider the term *cast* more appropriate.

but anyone who has attempted to collect wasp nests without damage to them appreciates their fragility. Even when a nest is suspended from a tree or similar structure under natural conditions, it disintegrates in a few months' time after it has been deserted by the wasps. The most striking feature of the fossil in this connection is that the casts of all "cells" are complete in the preserved portion of the "nest". Because of the fragility of paper nests, it seems impossible for such regularity to be attained; if only a few cells were so preserved, in various parts of the fossil, Dr. Brown's determination of the fossil would seem more probable.

Possibly some method of preservation radically different from that mentioned above can be given in explanation of the "nest"; but our geological associates have been unable to suggest one.

Apart from the difficulty of explaining the preservation of a paper nest, there are several aspects of the fossil which are not at all characteristic of a wasp's nest. Since the fossil shows almost no "structure", comparisons between it and nests of living wasps are very hard to make. Dr. Brown was consequently led to his conclusion by "general appearance and analogy". The following differences between the fossil and the nests of Recent social wasps seem to us to be significant: a) The dome-shaped tops of the projections were considered by Dr. Brown to be the casts of bottoms of the cells. Now, although the top or open ends of the cells in a wasp nest show a regular arrangement, the bottoms or lower ends are irregularly arranged, as can easily be seen in sections or when the paper covering over this part of the nest is removed. Consequently, the regular arrangement of the lower ends of the cells in the fossil is not at all suggestive of a wasp nest.[3] b) The bottoms of the cells of Vespid nests are not dome-shaped, as in the fossil, but are flattened or angular. Also the level of the bottoms of the various cells is irregular, so that casts of them would be variable in height as well as in shape. This is not true of the fossil, however,

[3]The regularity of the "cells" in the fossil resembles the structure of the nests of some Meliponidæ and bumble-bees more than that of a wasp. There are other objections, however, which eliminate these as a possible interpretation of the fossil.

for the projections are remarkably uniform in shape and height. c) The cells of Vespid nests tend to radiate from the base of the nest, the individual cells being distinctly wider at their openings than at their bases. In the fossil the "cells" have a constant width for their entire length and there is no indication of a radiating arrangement. d) the walls in the cells of a wasp nest are of paper thickness only; in the fossil the substance between the "cells" is nearly as thick as half the diameter of the "cells".

These discrepancies between the fossil and the structure of known Recent Vespid nests, in addition to the difficulty of accounting for preservation of such a fragile structure, lead us to reject Dr. Brown's conclusions regarding this specimen. We believe the interpretation of *Celliforma favosites* is altogether too uncertain and problematical for it to be accepted as a Cretaceous wasp nest without more proof than has been offered and in view of the total absence of remains of fossil Vespidae, either social or solitary, from that period.

We might point out that there is some superficial resemblance between Dr. Brown's fossil and certain "fossil nests" which have been recently described from Uruguay by F. Lucas Roselli,[4] and which are thought to be of Cretaceous age, also. We refer particularly to the fossil named *Uruguay auroranormai,* which shows a somewhat similar arangement of cells of even diameter from top to bottom, ending in dome-shaped bases; the cells are not represented by casts, however, but are hollow, with their own walls preserved. If such structures were filled with sand or mud, they might presumably after hardening become "fossils" similar to that described by Dr. Brown. Some of the Uruguayan nests are claimed by Roselli to be the work of solitary diplopterous wasps, although this seems to us extremely problematical. Without examining these nests and knowing more about the conditions under which they occur, we cannot of course discuss them further; but they look suspiciously like nests built by certain Recent solitary bees. The female of the European *Halictus quadricinctus,* for example, digs a spacious chamber at the end of a tunnel in the soil, in which she

[4]Boletin de la Sociedad Amigos de las Ciencias Naturales Kraglievich-Fontana", vol. I, pt. 2, September 1938, pp. 72-102.

constructs as many as 16 to 20 earthern cells, arranged in a crude comb.[5]

Since incorrect and misleading statements about the geological age of social insects are common in both entomological and paleontological literature,[6] we include here a summary of the evidence bearing on the subject. Parental care of young occurs in many groups of insects (e.g., Embiaria, Hemiptera, Dermaptera, etc.), but truly social habits among Recent insects are confined to members of two orders, Isoptera and Hymenoptera. The earliest Isoptera known are from the Eocene period and the group is well represented in the Baltic amber (Oligocene). Since only the winged or sexual forms have been found fossil, we have no factual knowledge that these Tertiary species were social. However, inasmuch as the social organization of the termites is more highly developed than that of any other insects, it was probably well advanced even in the early Tertiary. This conjecture is supported by the presence in the amber species of the transverse suture along which the wing breaks after the insects have swarmed.

The Hymenoptera as a whole have been found as far back as the Jurassic, from which Siricoid and parasitic types have been described. Social habits have been independently developed many times within the order, as Wheeler has pointed out, but none of the social families have been found in strata below the Eocene. The Formicidæ (ants), which are the most highly social of the Hymenoptera, are represented in several Eocene beds. The presence of workers among these Eocene species is conclusive proof that the ants had a well-developed society by that period. This is not surprising, inasmuch as caste differentiation of the Baltic amber ants was as advanced as that of Recent Formicidæ. The social history of the bees (Apoidea) has clearly been very different from that of the ants, for as shown by several Hymenopterists, social habits have been developed on at least three

[5]Bischoff has figured a nest of this solitary bee (Biologie der Hymenopteren, 1927, p. 222, fig. 94.)

[6]For example, a recent edition of a standard text of historical geology states that termites and "social ants" occur in Jurassic strata. Actually, neither of these groups has been found in rocks older than the Eocene.

different occasions among these insects. The oldest bees known are from the Baltic amber (Oligocene), and some of these belong to highly social families (Bombidæ, Apidæ). None of the described amber bees, however, can be placed in existing genera of these social families.[7] Furthermore, since none of the amber bees have been positively identified as workers, there is again no factual evidence that they were social. The social wasps (Vespidæ) have a much weaker social organization than the termites or ants, and as in the case of the bees, social habits have arisen several times among the Vespidæ and even within certain genera of the family (*e.g., Stenogaster*). The oldest known Vespidæ are from the Eocene, and several Baltic amber species (apparently) belong to existing genera which include social species. This fact by itself does not, however, prove the existence of social habits among the Eocene or Oligocene wasps. Recent Vespidæ have no structural characteristics definitely separating all social species from the solitary ones. Moreover, Recent social Vespidæ scarcely ever show structural differences between the workers and the queen.

As the geological record now stands, therefore, there is definite proof of the existence of social insects only as far back as the Eocene. Furthermore, only one Recent family, the Formicidæ, has a social history extending into that period. The termites have probably had a well developed society for at least as long a time as the ants, though there is no paleontological evidence for that conclusion. The bees and wasps, also, may have had a social development extending beyond the Eocene, but no fossil evidence for that has been found, and the nature of their present social structure is decidedly against that possibility.

[7] A true *Bombus, B. proavitus* Cock., has however been found in the Miocene of Washington (state).

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